

Partial dietary separation between coexisting cohorts of *Yllenus arenarius* (Araneae: Salticidae)

Maciej Bartos: University of Lodz, Department of Teacher Training and Studies of Biological Diversity, Banacha 1/3, 90-237 Lodz, Poland. E-mail: bartos@biol.uni.lodz.pl

Abstract. A long-term diet analysis of a polyphagous jumping spider *Yllenus arenarius* Menge 1868 (13 yr, $n = 321$ prey items) was carried out in Central Poland. Due to the spider's long life cycle two cohorts are present for the whole season and for one month three cohorts coexist, which allowed me to investigate whether coexisting spiders feed on similar or different prey. Diets of spiders from these three cohorts were found to differ in three aspects: prey taxa, prey diversity and prey size. Spiders from each cohort maintained a fairly constant ratio between prey size and their own size throughout the life cycle, which resulted in dietary separation between individuals from coexisting cohorts. Such mechanisms may reduce the intensity of competitive interactions between coexisting spiders.

Keywords: Spider, diet, prey, polyphagy, intraspecific competition, development, Poland

Diets of spiders that do not build webs are poorly known (Nentwig 1987). Even though spider prey has gained considerable attention over the last decades, generally due to the potential exploitation of spiders as agents of pest control, the research has been dominated by the studies of web-building spiders (reviewed in Wise 1993). Such bias generally results from the studies of cursorial spiders' diets requiring considerably longer to obtain the same number of data than studies of web-builders' diets. The prey items of non-web-building spiders are collected by direct observation and by inspection of individual spider's mouthparts, while in the case of web-building spiders, their webs, which function as passive traps continuously accumulating prey, are inspected (Nentwig 1987). For these reasons the time of prey retention in the case of cursorial spiders is usually shorter, and hunting success is lower than in web-builders (Edgar 1970; Jackson 1977).

Considerable data would not only describe a particular spider's diet, but might also allow us to analyze age- and size-dependent changes that occur in a spider's lifetime. Spiders that actively hunt their prey are known to keep a fairly constant ratio between prey size and their own size (Nentwig & Wissel 1986; Nentwig 1987); therefore, it may be expected that newly hatched spiderlings and much larger adult individuals will have different diets. Furthermore, more general conclusions on diet-related phenomena, such as food competition, could be drawn. There is a strong bias in the type of competitive interactions researched, as the research has been dominated by studies of interspecific competition (Horton & Wise 1983; Riechert & Cady 1983; Nentwig 1983, 1986; Nyffeler & Sterling 1994). Very few studies have been focused on intraspecific competition, particularly in cursorial spiders (Wise & Wagner 1992; Wagner & Wise 1996; reviewed in Wise 1993).

Several characteristics of *Yllenus arenarius* Menge 1868 make this species especially useful to study both the diet of different age groups and possible competitive relationships between coexisting cohorts. Firstly, due to the longest life cycle reported for any jumping spider, three cohorts from three successive years coexist for 1 mo annually, and for the rest of the season spiders from two cohorts are present (Bartos 2005). The lifespan reaches up to 770 days. Juveniles emerge from

eggs laid in sub-sand nests in early June, and females in their third year of life, which produce the eggs, die by the end of June.

Secondly, the spider inhabits a simple environment, which makes the interactions between different species that occur in the habitat more transparent. *Yllenus arenarius* is a stenotopic species, which in Central Europe is mostly limited to *Spergulo-Corynephorum* habitat, in particular to the initial stage of dune succession, where sand areas are sparsely vegetated by grey hair-grass (*Corynephorus canescens*) with numerous, unvegetated patches in between (Merkens 2000; Logunov & Marusik 2003). Such habitat is characterized by a limited number of niches, low nutrient supply and adverse temperature and humidity conditions (Almquist 1970, 1971; Bonte et al. 2000).

Thirdly, *Y. arenarius* is a dominant day-active arachnid predator in its habitat, which suggests that intraspecific interactions can be strong and may be detectable. The spiders' populations reach densities of up to about five individuals/m², and in comparison with other day-active invertebrates of comparable size, they are outnumbered only by those of *Formica cinerea* (Hymenoptera: Formicidae) (Bartos, pers. observ.).

Finally, different aspects of the spider's biology, including the predatory behavior of different age groups, have already been described, which provide important background information for interpretation of possible differences between spider age groups. *Yllenus arenarius* is a sit-and-wait predator that awaits a prey that lands in its proximity or a prey that approaches the predator by land. The spiders feed on a wide spectrum of invertebrates (Bartos 2004) and possess complex prey-specific predatory strategies (Bartos 2002, 2007). Inexperienced spiders are able to identify different prey types and express a nearly complete spectrum of prey-specific behaviors characteristic for adults. The spider's hunting pattern changes only moderately with age (Bartos 2008).

The aim of this research was to investigate whether individuals from coexisting cohorts of *Y. arenarius* have different diets, and if so, which mechanisms may be responsible for such a dietary separation. For this purpose I studied the spider's lifetime diet, with particular focus on the

period when three cohorts coexisted in the field. I hypothesized that the relative body size of spiders would be the main determinant of captured prey. Thus I compared the proportion of prey changing its size during the season, the Acrididae, among cohorts.

METHODS

Procedure.—During 13 years (1997–2009), 321 items of prey were collected from spiders in 11 inland dunes in Central Poland. Most prey ($n = 291$) were collected from one site – Kwilno (51°59' N, 19°30' E). This site was visited at least once every two weeks throughout the season. In June data were collected on a daily basis; therefore, the number of records is much higher in this month.

Prey.—The prey items were collected during field surveys from the chelicerae of *Y. arenarius*. During each survey, the ground surface was thoroughly searched, and all spiders encountered visually were captured in transparent glass vials. Each vial was then inspected. Any prey that was found in a spider's chelicerae was measured and preserved in ethanol for further determination. Prey's body length was measured from the tip of the head to the end of the abdomen. In this study the prey of *Y. arenarius* is analyzed on higher taxonomical levels (orders and families).

Spiders.—In each year of study individuals from three cohorts, hatched in three successive years, were recognized. These were: a) individuals from the cohort hatched in June of that particular year, described as juveniles in the first year of life (juv-1); b) individuals from the cohort hatched in June of the previous year, described as juveniles in the second year of life (juv-2), or adults in the second year of life after the final molt (ad-2) and; c) individuals from the cohort hatched in June two years before the year of study, described as adults in the third year of life (ad-3). The prey of adults in the second year of life (ad-2) was used only in the lifetime diet analysis, and this group of spiders was not discussed separately. Spiders with prey were assigned to cohorts on the basis of their size and maturity according to a previously developed method (Bartos 2005). Males of *Y. arenarius* died earlier than females and usually did not survive longer than mid-May; therefore, in July only females were captured with prey.

Measurements were taken on live spiders, which were then released back into the field. Three body measurements were taken: abdomen length, abdomen width and eye field width. Abdomen length and abdomen width are measurements of elastic body parts; therefore, they are good indicators of spider size and condition. Eye field width (distance between lateral margins of posterior lateral eyes) is a measurement of a hard structure on the spider's carapace. It does not depend on temporary hunger status and therefore it is a proper indicator of age (Bartos 2005).

Voucher specimens of *Y. arenarius* are deposited in the Archaeological Collection of the Department of Zoology, University of Podlasie, Siedlce, Poland.

Data analysis.—All statistical procedures, namely the chi-square test, Kruskal-Wallis ANOVA and Pearson correlation followed those described by Zar (1984). Natural logarithm-based Shannon-Wiener diversity indices (H') and t -tests for differences between cohorts were calculated according to Magurran (1988). Data are presented as mean \pm SD.

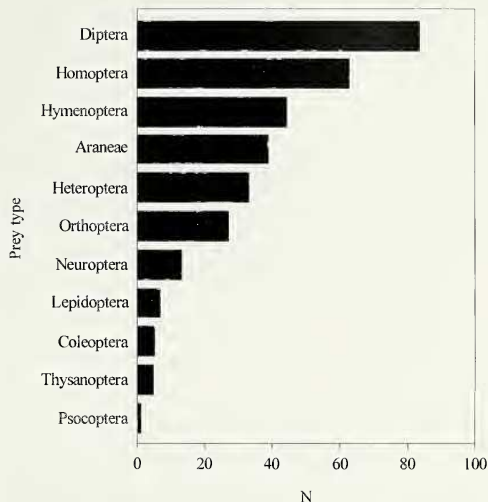


Figure 1.—Absolute frequency of 11 prey orders in the diet of *Yllenus arenarius* ($n = 321$ prey).

RESULTS

Lifetime diet of *Y. arenarius*.—Ten insect orders and one arachnid order were recorded in the diet of *Yllenus arenarius* (Fig. 1). Only imagoes were present for Diptera, Hymenoptera, Coleoptera, Thysanoptera and Psocoptera. Homoptera, Araneae, Heteroptera and Orthoptera were represented by both imagoes and juveniles. Neuroptera and Lepidoptera were represented only by larvae.

There was a wide diversity in the size of prey captured by *Y. arenarius*. A positive correlation was found between spider size and prey size (Fig. 2). All three spider body measurements show similar relationships. The correlation was stronger between spider abdomen width and prey length ($r = 0.68$, $P < 0.05$, $n = 259$) and between spider abdomen length and prey length ($r = 0.67$, $P < 0.05$, $n = 259$) than between spider eye field width and prey length ($r = 0.60$, $P < 0.05$, $n = 259$). The ratio of prey size to spider size shows that about 80% of the prey in the spiders' diet is smaller than the spiders' own body size. Body lengths of most prey items ranged from 40% up to 100% of the spider's body length, with the most numerous group almost as long as the predator.

Diets of spiders from three coexisting cohorts.—Prey composition in the spiders' diet varied throughout the year. The differences between diets of spiders from coexisting cohorts were especially apparent in June, when three cohorts were present. The differences were manifested in three aspects: prey size, prey taxa and prey diversity.

Prey size: Spiders from the three cohorts exploited invertebrates of different sizes as prey (Kruskal-Wallis ANOVA, $H_{(2,135)} = 58.39$, $P < 0.0001$) (Fig. 3). If the prey length was standardized on spider length, the relationship disappeared (Kruskal-Wallis ANOVA, $H_{(2,135)} = 5.50$, $P > 0.05$).

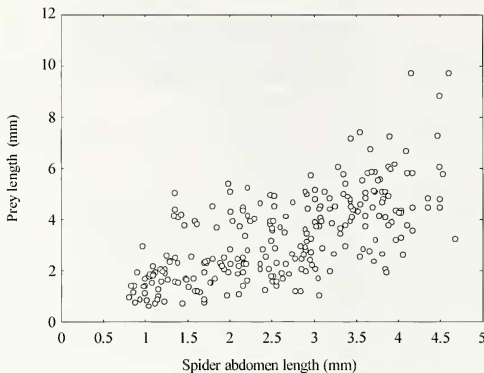


Figure 2.—Relationship between abdomen length of *Yllenus arenarius* and its prey total body length.

Prey taxa: Different numbers of arthropod orders and different frequencies of prey from each order were found in the diets of spiders from coexisting cohorts (Fig. 4). Some prey taxa were present in the diet of all cohorts, but they occurred with different frequencies. The proportion of Homoptera dropped with age ($\chi^2 = 16.07$, $df = 2$, $P < 0.001$); a similar pattern was observed for Diptera ($\chi^2 = 8.45$, $df = 2$, $P < 0.02$). The proportion of Hymenoptera increased with age ($\chi^2 = 6.07$, $df = 2$, $P < 0.05$). A limited number of prey taxa: Aphididae (Homoptera), Thysanoptera and Orthoptera, were found in the diets of only certain cohorts. Differences in the frequency of Aphididae were the most pronounced ($\chi^2 = 33.34$, $df = 2$, $P < 0.0001$). This group comprised 46% of all prey of juv-1 ($n = 35$) and 11% of all prey of juv-2 ($n = 82$), but did not occur in the diet of ad-3 ($n = 43$). The smallest of all prey – specimens from the order Thysanoptera – were found only in the diet of juv-1 ($\chi^2 = 11.18$, $df = 2$, $P < 0.01$). Orthoptera occurred only in the diets of juv-2 and ad-3 ($\chi^2 = 11.83$, $df = 2$, $P < 0.01$). Differences in the frequency of other prey orders (Heteroptera, Araneae, Coleoptera, Neuroptera and Lepidoptera) were not significant.

Prey diversity: The diets of spiders from coexisting cohorts differed according to their diversity (Fig. 4). The diet of juv-1 was the least heterogeneous ($H' = 1.293$). These spiders consumed prey from six insect and arachnid orders. The most frequent prey taxa were Homoptera and Diptera, with a small number of Thysanoptera and other negligible prey. Spiders in the second year of life (juv-2) were characterized by a more diverse diet ($H' = 1.857$), consisting of prey from eight orders. The highest diversity was found in the diet of the oldest spiders (ad-3) ($H' = 1.939$). Diets of both juv-2 and ad-3 consisted of a wide range of prey in relatively similar proportions, and their diversity indices were similar ($t_{0.05; 126} = 0.70$, $P > 0.05$); therefore, the data were pooled. The index of prey diversity of juv-1 differed from the index based on pooled data of juv-2 and ad-3 and subsequently compared with the index of the juv-1 ($t_{0.05; 161} = 3.76$, $P < 0.001$).

Changes in the frequency of Acrididae over three months.—Acrididae were found only from April to June and only in the

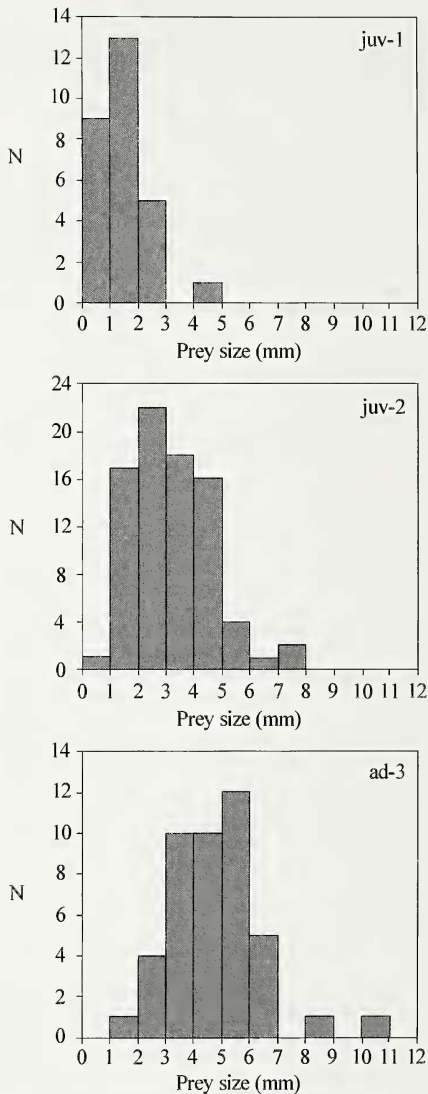


Figure 3.—Size distribution of prey captured by spiders from three cohorts of *Yllenus arenarius* coexisting in June.

diet of juv-2 and ad-3 (Fig. 5). The youngest spiders (juv-1) did not hunt this type of prey. In June, when the spiders hatched, Acrididae were already four times as long as the spiders. Although in both older cohorts (juv-2 and ad-3) the frequency of Acrididae dropped over time, the fraction of this

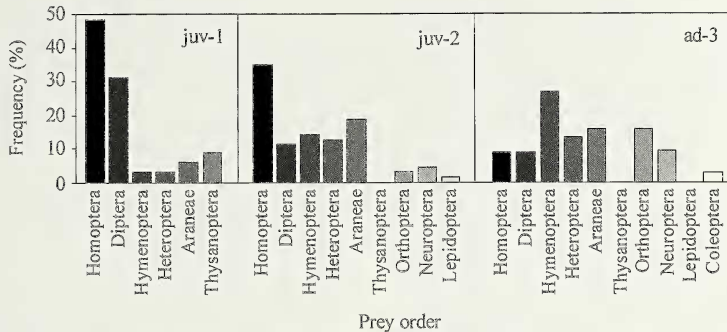


Figure 4.—Relative frequency of 10 prey orders captured by spiders from three cohorts of *Yllenus arenarius* coexisting in June. For juv-1, $n = 35$; for juv-2, $n = 82$; for ad-3, $n = 46$.

prey type was different, because in the diet of juv-2 it occurred from April, and in the diet of ad-3 it did not occur before May. As a consequence the same pattern was observed in both cohorts, but there was a switch in time between them (Fig. 5). In April Acrididae constituted almost 50% of all prey of juv-2 ($n = 9$), but they were totally absent in the diet of ad-3 ($n = 16$) ($\chi^2 = 11.83$, $df = 1$, $P < 0.01$). In May there were no significant differences between frequencies of Acrididae in the diets of juv-2 and ad-3, but in June the differences were present again ($\chi^2 = 10.86$, $df = 2$, $P < 0.005$).

DISCUSSION

The natural diet of *Yllenus arenarius* is typical for polyphagous salticids (e.g., Jackson 1977; Dean et al. 1987; Nentwig 1987; Young 1989; Guseinov 2005). The spider's diet composition may directly reflect the frequency of different prey available in the field or may result from the spider's preference, but to answer this question would require additional studies, as suggested by Huseynov et al. (2008). The spider's diet consisted mainly of invertebrates that possess the ability to move efficiently from one place to another (both imaginal and larval stages). These were winged imagoes of holometabolous insects (Diptera, Hymenoptera), larvae and imagoes of hemimetabolous insects (Homoptera, Heteroptera,

Orthoptera) possessing jumping legs or wings that enable effective locomotion, and Araneae that are good runners. Slowly and inefficiently moving holometabolous larvae of Lepidoptera and Neuroptera were relatively rare, which suggests that they may be accidental prey.

Data collected in the current study and other studies of spider prey suggest a correlation between the spider's size and its prey's size (Nentwig & Wissel 1986; Nentwig 1987). Such a relationship may result in the occurrence of different prey taxa in a spider's diet at different stages of its life cycle. As spiders' body sizes change during development, young (small) spiders and adult (several times larger) spiders may feed on, at least partially, different prey taxa. On the other hand, since prey body sizes may also significantly change during their development, some prey growing more quickly than spiders may vanish from the diet of a particular cohort of spiders, even in a short time-scale.

Spiders from coexisting cohorts were found to exploit different types of prey. This phenomenon was especially clear in June, when individuals from these three groups cohabited in the field (Fig. 4). Several prey taxa were only captured by spiders from certain cohorts. These were Thysanoptera (unique diet element of the youngest spiders) and Acrididae — present in diets of only juv-2 and ad-3. Other taxa (e.g.,

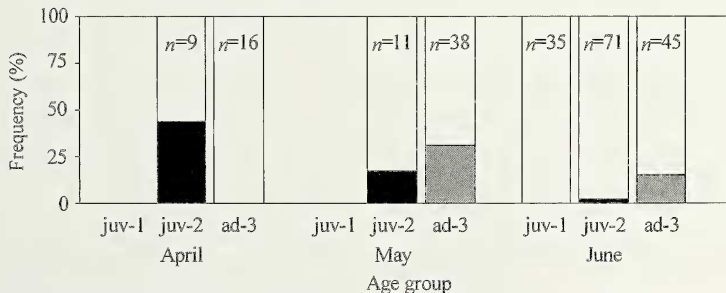


Figure 5.—Comparison of the relative frequency of Orthoptera captured in April, May and June by three cohorts of *Yllenus arenarius*; lack of bars in April and May indicate the absence of juv-1 in this period; juv-2 are indicated by black bars; ad-3 are indicated by grey bars.

Homoptera, Diptera and Hymenoptera) were preyed upon by spiders from all cohorts, but they occurred in the diets at different frequencies.

Differences between the diets of spiders from the three cohorts indicate changes in prey composition over a spider's life. Diet breadth becomes wider with age. Spiders in their first month of life (juv-1) feed on few prey types, which are captured in relatively high numbers. The youngest spiders have the least variable diet, in comparison to balanced and diverse diets of the two older cohorts (Fig. 4). These are mainly the smallest specimens and the youngest larval stages of hemimetabolous insects, many with limited motility. Such groups as Aphididae and Thysanoptera are largely ignored by older spiders (Bartos unpubl. results), but constitute a significant proportion of prey items of the youngest generation (Fig. 4). This distribution can be partially explained by the small size of the prey, since older spiders may prefer larger prey (Fig. 3). It is also possible that the smallest, often less active, prey is relatively easy to capture by inexperienced spiders or that some prey taxa (Aphididae in particular) are intentionally avoided by older, more experienced spiders due to the prey's low food quality and acquired aversion (Edwards & Jackson 1994; Toft 1995, 1999; Toft & Wise 1999). A similar reaction is known for aphid prey consumed by naive but not by experienced spiders (Toft 1997).

The majority of prey fell within 40% up to 100% of the predator's size, which is in accordance with general prey-size acceptance rates for other spiders that do not build webs (Nentwig & Wissel 1986; Nentwig 1987). Some prey items were smaller or larger than this range, sometimes even more than twice as long as the spider. The size extremes were exceptional, and a preference for a certain prey sizes was apparent.

The changes in frequency of Acrididae seem to be an example of the prey growing more quickly than the spider. Acrididae, which hatch in April, were not found in the diet of *Y. arenarius* later than in June. These insects are known to grow rapidly, and in July they become larger than the oldest and largest spiders from the ad-3 cohort (Bartos unpubl.). In June Acrididae may become too large for juv-2, while they may still be in a suitable size range for ad-3. This would explain why there are characteristic differences in the frequencies of Acrididae in the diets of spiders from two coexisting cohorts, as if there was a one-month-long shift in time (Fig. 5). The rapid growth of Acrididae is accompanied by a drop in their population density (Bartos unpubl.), which may partially explain the drop in number of Acrididae in the diet of spiders from both older cohorts (juv-2 and ad-3) toward summer.

Results presented here suggest that three coexisting cohorts of *Y. arenarius* exploit invertebrates of different sizes as prey (Figs. 2, 3). If the prey length, however, is standardized on spider length the relationship disappears, which implies that the spiders maintain a fairly constant ratio between prey size and their own size throughout their whole life. If predators of different sizes select prey items of relatively fixed size proportion to their own size, they may consume different prey types (Branch 1984). Fixed prey-size ratio may also result in at least partial food-niche separation in *Y. arenarius*. Such a mechanism may reduce the intensity of competitive interactions and may be responsible for the high densities of *Y. arenarius* observed in the field.

ACKNOWLEDGMENTS

I would like to thank two anonymous reviewers for their work and valuable comments that have improved the quality of the initial manuscript. This research was supported by the Polish Ministry of Scientific Research and Information Technology (grants: SCSR 6P04F07215, SCSR 3P04F05822, SCSR 2P04F02830) and the University of Lodz.

LITERATURE CITED

- Almqvist, S. 1970. Thermal tolerances and preferences of some dune-living spiders. *Oikos* 21:230-236.
- Almqvist, S. 1971. Resistance to desiccation in some dune-living spiders. *Oikos* 22:225-229.
- Bartos, M. 2002. Distance of approach to prey is adjusted to the prey's ability to escape in *Yllenus arenarius* Menge (Araneae, Salticidae). Pp. 33-38. *In* European Arachnology 2000. (S. Toft & N. Scharff, eds.). Aarhus University Press, Aarhus, Denmark.
- Bartos, M. 2004. The prey of *Yllenus arenarius* (Araneae, Salticidae). *Bulletin of the British Arachnological Society* 13:83-85.
- Bartos, M. 2005. The life history of *Yllenus arenarius* (Araneae, Salticidae) - evidence for sympatric populations isolated by the year of maturation. *Journal of Arachnology* 33:214-221.
- Bartos, M. 2007. Hunting prey with different escape potentials - alternative predatory tactics in a dune-dwelling salticid. *Journal of Arachnology* 35:499-509.
- Bartos, M. 2008. Alternative predatory tactics in a juvenile jumping spider. *Journal of Arachnology* 36:300-305.
- Bonte, D., M. Hoffmann & J.-P. Maelfait. 2000. Seasonal and diurnal migration patterns of the spider fauna of coastal grey dunes. *Ekologia (Bratislava)* 19:5-16.
- Branch, G.M. 1984. Competition between marine organisms: ecological and evolutionary implications. Pp. 458-627. *In* Oceanography and Marine Biology: an Annual Review, Volume 22. (M. Barnes, ed.). Aberdeen University Press, Aberdeen, UK.
- Dean, D.A., W.L. Sterling, M. Nyffeler & R.G. Breene. 1987. Foraging by selected spider predators on the cotton fleahopper and other prey. *Southwestern Entomologist* 12:263-270.
- Edwards, G.B. & R.R. Jackson. 1994. The role of experience in the development of predatory behaviour in *Phidippus regius*, a jumping spider (Araneae, Salticidae) from Florida. *New Zealand Journal of Zoology* 21:269-277.
- Edgar, W.D. 1970. Prey and feeding behaviour of adult females of the wolf spider *Pardosa amentata* (Clerck). *Netherlands Journal of Zoology* 20:487-491.
- Guseinov, E.F. 2005. Natural prey of the jumping spider *Salticus tricinctus* (Araneae, Salticidae). *Bulletin of the British Arachnological Society* 13:130-132.
- Huseynov, E.F., R.R. Jackson & F.R. Cross. 2008. The meaning of predatory specialization as illustrated by *Aelurillus m-nigrum*, an ant-eating jumping spider (Araneae: Salticidae) from Azerbaijan. *Behavioural Processes* 77:389-399.
- Horton, C.C. & D.H. Wise. 1983. The experimental analysis of competition between two syntopic species of orb-web spiders (Araneae: Araneidae). *Ecology* 64:929-944.
- Jackson, R.R. 1977. Prey of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). *Journal of Arachnology* 5:145-149.
- Logunov, D.V. & Y.M. Marusik. 2003. A revision of the genus *Yllenus* Simon, 1868 (Arachnida, Araneae, Salticidae). KMK Scientific Press Ltd., Moscow.
- Magurran, A.E. 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, New Jersey.
- Merkens, S. 2000. Epigeic spider communities in inland dunes in the lowlands of Northern Germany. Pp. 215-222. *In* European Arachnology 2000. (S. Toft & N. Scharff, eds.). Aarhus University Press, Aarhus, Denmark.

- Nentwig, W. 1983. The prey of web-building spiders compared with feeding experiments (Araneae: Araneidae, Linyphiidae, Pholcidae, Agelenidae). *Oecologia* 56:132–139.
- Nentwig, W. 1986. Non-webbuilding spiders: prey specialists or generalists? *Oecologia* 69:571–576.
- Nentwig, W. 1987. The prey of spiders. Pp. 249–263. *In* *Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Nentwig, W. & C. Wissel. 1986. A comparison of prey lengths among spiders. *Oecologia* 68:595–600.
- Nyffeler, M. & W. Sterling. 1994. Comparison of the feeding niche of polyphagous insectivores (Araneae) in a Texas cotton plantation: Estimates of niche breadth and overlap. *Environmental Entomology* 23:1294–1303.
- Riechert, S.E. & A.B. Cady. 1983. Patterns of resource use and tests for competitive release in a spider community. *Ecology* 64:899–913.
- Toft, S. 1995. Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *Journal of Applied Ecology* 32:552–560.
- Toft, S. 1997. Acquired food aversion of a wolf spider to three cereal aphids: intra- and interspecific effects. *Entomophaga* 42:63–69.
- Toft, S. 1999. Prey choice and spider fitness. *Journal of Arachnology* 27:301–307.
- Toft, S. & D.H. Wise. 1999. Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* 119:191–197.
- Wagner, J.D. & D.H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology* 77:639–652.
- Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge, UK.
- Wise, D.H. & J.D. Wagner. 1992. Evidence of exploitative competition among young stages of the wolf spider *Schizocosa ocreata*. *Oecologia* 93:7–13.
- Young, O.P. 1989. Field observations of predation by *Phidippus audax* (Araneae: Salticidae) on arthropods associated with cotton. *Journal of Entomological Science* 24:266–273.
- Zar, J.H. 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.

Manuscript received 21 September 2010, revised 10 February 2011.